ABSTRACTION AND ENCODING OF SENSORY INFORMATION

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This research program was designed toward the functional/anatomical description of the neural movement detection system with the end product an insight into how behavior can be described in the information processing of known anatomical nerve networks. The research concentrated on the processes of reception by photoreceptors, and processing of visual information by interneurons in the optic lobe, brain and thoracic ganglion. For the first time a system of movement detectors has been identified. There are possibly as few

20. ABSTRACT Contd.

as 30 cells per animal which are command fibers for the control of flights. The horizontal and vertical movement detection systems are distinct anatomically, physiologically and behaviorally.

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TABLE OF CONTENTS

i. ABSTRACT i

1. Introduction 1

2. Behavioral Studies 3

3. Anatomical Studies 5

4. Electrophysiological Studies 8

5. References 13

i. ABSTRACT

This research program has been designed toward the functional/anatomical description of the neural movement detection system in flies. The end product of such research is insight into how behavior can be described in the information processing of known anatomical nerve networks.

This research has concentrated upon the processes of reception by the photoreceptors, and processing of visual information by interneurons in the optic lobe, brain and thoracic ganglion of insects.

1. Introduction

The ultimate goal of the neurobiologist is the attainment of a structural and functional description of how the nervous system mediates behavioral responses. Since the function of nerve cells and their interactions through synapses seem to be similar throughout the animal kingdom including man, it is reasonable to study at first relatively simple neural networks in order to come to an understanding of how they work. The information so obtained forms a basis for investigations of more complex neural systems. The ultimate goal is to understand how the human brain functions.

Neurobiologists are thus in constant search for the "right" experimental preparation in order to give answers in specific research areas. For the goal stated above, 1) an experimental preparation should have a behavioral repertoire that is complex enough to be interesting, yet not so complex that it is not experimentally accessible, 2) the behavior of the animal must be amenable to quantitative experimental study, 3) the single neurons should be directly accessible to electrophysiological recording, and 4) the neurons from which electrical recordings are taken must be identifiable.

Such an "ideal" preparation is hard to find. For example, the important concept of lateral inhibition came from studies of the compound eye of the hoseshoe crab Limulus. An important feature of lateral inhibition is the enhancement of contrast in a visual pattern as perceived by the animal. In other words, the contrast in a visual stimulus which is reduced by the low pass filter characteristics due to the receptive fields of the receptors can be partially or completely compensated for by the mechanism of lateral inhibition. Attempts to demonstrate the behavioral use of the eye have not been very successful and hence the role of lateral inhibition in behavioral responses of this animal remains unexplained. Investigations of the visual systems of the cat, monkey, frog and several other vertebrates have revealed much about the ab-

straction of information from the visual environment. But, these systems have a high degree of complexity so that the information flow has not yet been studied throughout the visual system. Furthermore, correlation with behavioral responses is difficult, since these responses are rather complex and not easily quantifiable. A large number of people have recorded from cells in the ganglia of molluscs, mainly restricting themselves to, and studying the control of, motor output. These preparations are particularly valuable for the study of cell-cell interactions and the motor control of some simple behavioral responses. We believe, and have demonstrated, that in the fly or bee we have an opportunity to extend such an approach to a much more complex yet quantified behavioral reaction from the sensory input to the motor output.

Studies of the behavior of flies and honeybees are classics in the field. For example, the behavioral responses to color or to object movement are very steriotyped responses and have been studied to the extent that they can be predicted (section I , 2).

Some information about the neural processing of visual information leading to behavioral responses has been obtained from extracellular recordings (section I , 4), but much more information can be obtained from intracellular recordings since the slow potential changes accompanying the spike initiation can be studied, too. Thus the subthreshold activity is also obtained. We have demonstrated that it is possible to obtain intracellular recordings from neurons whose axons have diameters ranging from 1-3 microns. We were able to stain such cells by iontophoretic injection of fluorescent dyes after obtaining intracellular records (Dvorak, Bishop and Eckert, 1974).

In the following paragraphs evidence will be presented that:

1. Flies and bees have complex, visually mediated, yet quantitatively describable behavioral responses (section I , 2).
2. The nervous systems of flies and bees are complex, yet highly organized in a periodic fashion thus restricting the number of <u>different</u> neurons to be identified histologically and characterized electrophysiologically (section I , 3).
3. The anatomy of the visual systems of flies and bees have already been described to a high degree so that iontophoretically stained neurons can be identified anatomically (section I , 3).
4. The nervous systems of flies and bees are accessible to direct electrophysiological approach (section I , 4).

2. Behavioral Studies

Many behavioral responses to visual stimuli (generally called optomotor responses) e.g. movement towards or away from light, orientation to the plane of polarized light, following the direction of movement of an object or fixation of an object, have been the subject of thorough investigations throughout this century. Early studies (Gavel 1939; Hertz 1934) were followed by quantitative studies by Hassenstein and Reichardt (1956) on the beetle Chlorophanus (see also Reichardt und Varju 1959, Varju und Reichardt 1967). These experiments were performed by placing the animal into the center of a rotating drum which had black and white stripes on its inner surface. The animal, glued to a piece of cardboard and held by a small forceps, "walked" along a straw sphere with four Y-shaped intersections (generally called Y-maze globe). When walking along the globe, a continuous series of right and left choices had to be made by the animal. If there was no moving pattern presented to the animal, right and left choices were equal. If there were optomotor turning reactions, the proportions of right and left choices in the two directions provided a sensitive and quantitative measure of the strength of the optomotor reaction.

These experiments led to a mathematical model of movement perception for this insect, the beetle Chlorophanus, which predicted quantitatively the reaction to (even previously untested) changes of the parameters in the visual stimuli (see review Reichardt 1969).

This model consists of two cross-connected information input channels from two receptors and a common output channel to the motor system. It accounts for the functional properties of the physiological system in terms of an input-output relationship.

Subsequent studies on other insects, e.g. the bee Apis (Kunze 1961), the fruitfly Drosophila (Götz 1964-1973), the housefly Musca (Fermi und Reichardt 1963, review Reichardt 1969, Reichardt 1973, Eckert, 1970, 1972, 1973), the meal moth Ephestia (Kunze 1970) and even other arthropods, e.g. the ghost crab Ozypode (Kunze 1964) revealed that this model of movement perception is applicable to many arthropods. Studies similar

to those done on the optomotor reactions of walking animals were made on flying animals (fly, bee), either under an open loop condition or a closed loop condition (Reichardt 1973). In the closed loop condition the animal controls the movement of its environment. These experiments revealed, that the torque elicited by the fixed flying animal is different for object movement in opposite directions, that is frontad to caudad and vice versa. This accounts for the capability of the animal to fixate a vertically oriented striped object. Further investigations showed that there is a second system perpendicular to the one described above with similar properties for fixation on a horizontally oriented striped object. (Wehrhahn und Reichardt, 1973).

Gotz (review 1972) showed (by means of optomotor experiments) that the vertical and horizontal components of the movement of an object are perceived by two different movement detecting systems: The horizontal system conveys information to the muscular system of the legs and wings, thus controlling the difference between the locomotor forces on either side. The information from the vertical system is conveyed exclusively to the flight system controlling the sum of the locomotor forces on either side. The directionally selective motion detecting neurons (measured electrophysiologically) are grouped into two such systems, one group maximally excited by pattern movement in the vertical, the other by pattern movement in the horizontal direction (see section I , 4).

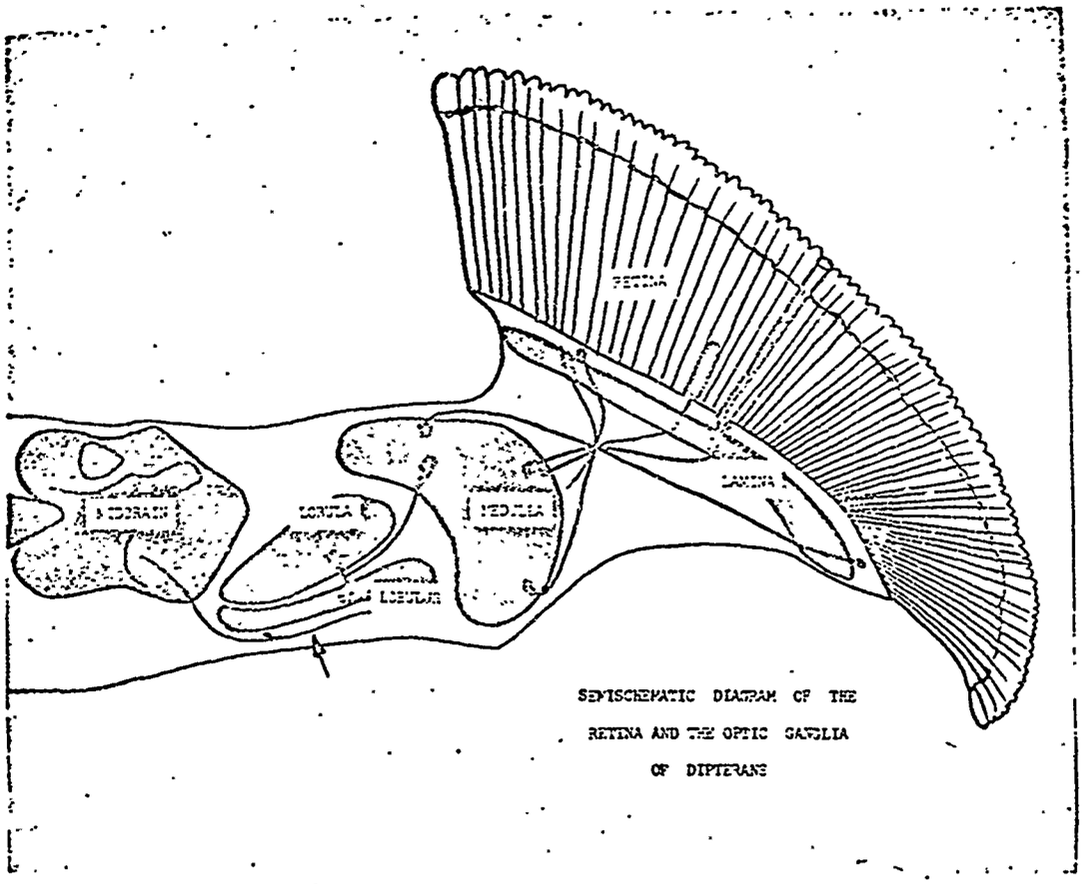


Figure 1. Semischematic diagram of the retina and the optic ganglia of dipterans. A few cells and axons are shown, demonstrating the crossing over of fibers in the external chiasma between Lamina and Medulla. The arrow points to the stained motion detecting cell shown in Figure 8.

3. Anatomical Studies

The organization of the fly's brain is shown in a semischematic diagram in figure 1. Principally, the same organization is found in the bee. The brain consists of several optic ganglia in which synaptic contacts are made. Connections between the ganglia are made by the axons of the nerve cells. The separation of regions in which synaptic contacts are made into several ganglia makes this system particularly interesting for the study of the processing of visual information for two reasons: 1) The single nerve cells participating in the uptake and processing of visual information are relatively easily accessible, and 2) since there is a periodic repetition of groups of nerve fibers within the ganglia and connecting chiasmas between the ganglia, only a limited number of different nerve cell types have to be studied.

Fibers in the third optic ganglion respond to moving patterns in a similar manner to the optomotor reactions of the whole intact animal. This implies that most of the processing of visual information for the optomotor response is achieved in the peripheral optic ganglia. Thus, we feel that this system is especially suitable for the study of neural correlates of behavioral responses. How far it might be possible to trace the output of this motion detection system to the motor output must remain open. The centrally located neurons, which connect the midbrain to the thoracic ganglion via the ventral nerve cord and deliver the input for the motorneurones, are joined by many other nerve fibers which are not part of the visual system.

The first comprehensive study of the neuroarchitecture of the optic lobes of flies and bees was a light microscopical study by Cajal and Sanchez (1915) using the reduced silver stain and Golgi impregnation techniques.

More recently the retina and optic lobes of the fly have been studied extensively by light and electronmicroscopical techniques (e.g. Braitenberg 1966; Boschek 1971, 1973, Campos-Ortega and Strausfeld 1973; Franceschini and Kirschfeld 197 ; Kirschfeld 1967; Kirschfeld and Franceschini 1969; Strausfeld 1971, 1973a, 1973b, 1974; Strausfeld and

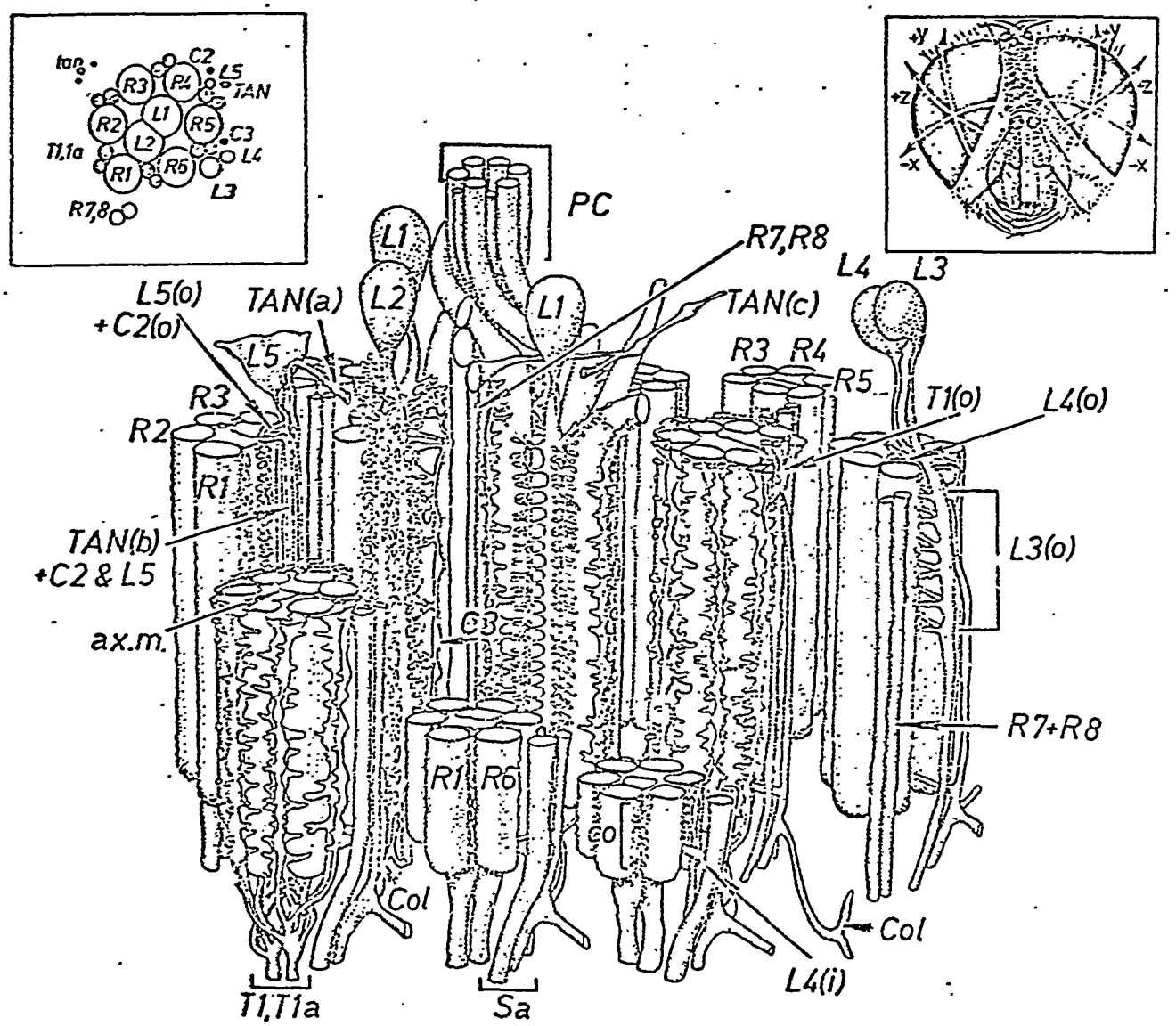


Figure 2. Schematic diagram of the Lamina of the housefly Musca domestica according to Strausfeld (1971). At PC the eight retinula cell axons of an ommatidium are shown as they emerge from the central end of an ommatidium and enter the lamina. Here each of the axons from retinula cells 1-6 (insert at top left) enters a different neurocartridge, the cluster unit of the lamina (shown in crossection in the insert at the top left). Retinula cells 7 and 8 (smaller axons) bypass the lamina and make their first synaptic contacts in the medulla. C, TAN, tan, T: tangential fibers; L1-L5: Second Order monopolar neurones; R1-R8: Retinula Cell Axons; Col: Collaterals; (i): inner collateral, (o) outer collateral; co: combs of L1; Sa: Satellite

Blest 1970; Strausfeld and Braitenberg 1970; Strausfeld and Campos-Ortega 1973; Trujillo-Cenoz 1965; a.o.). The most comprehensive study is the light microscopical investigation of Strausfeld. These studies are reported in several papers and are summarized in a forthcoming atlas.

The current consensus is that the fly's visual system is separated into two subsystems. The axons from retinula cells 1-6 (figure 2) make synaptic contacts in the first optic ganglion, the Lamina ganglionaris, in such a way that the input from six retinula cells, which are situated in six neighboring ommatidia and whose rhabdomeres share the same optical axis, converge upon the same lamina cartridge. In other words, the axons from those retinula cells which receive input from the same point in the environment make synaptic contacts with the same cells in the lamina, that is, certain monopolar second order neurones. In analogy to the optical superposition eye (Exner 1891), the convergence of light induced signals of the receptor cells in the lamina led to the term "neural superposition eye" (Kirschfeld 1967). The axons from the retinula cells 7 and 8 which lie in tandem position, bypass the lamina and end in different layers of the medulla. The orthogonal arrangement of microvilli in the rhabdomeres of cells 7 and 8 suggest a system for detecting the angle of polarized light. Behavioral experiments have led to the conclusion that this receptor system actually is capable of detecting the plane of linearly polarized light (Kirschfeld and Reichardt, 1970); whereas in the receptor system consisting of the retinula cells 1-6 this information is destroyed because of the "neural superposition" of the receptor potentials in the lamina cartridges.

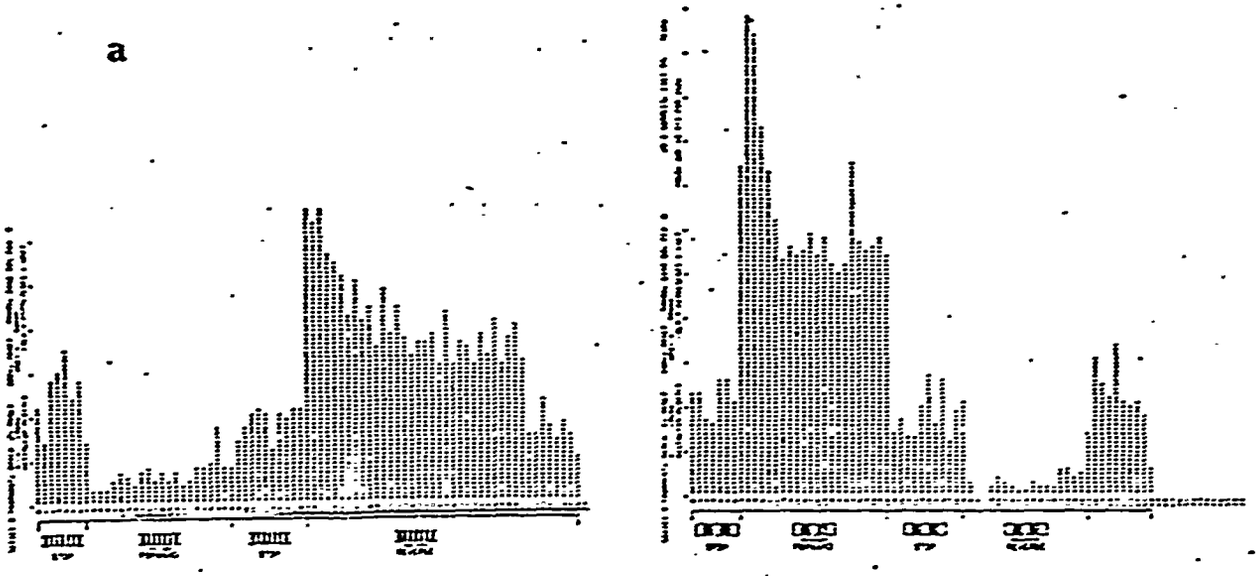
Strausfeld has described the structure and course of numerous cells in the lamina, medulla and lobula complex. One of Strausfeld's summary diagrams is reproduced in figure 2 in order to illustrate the detail to which the anatomy has been described. It is to be noted that this system, the lamina ganglionaris, is composed of spatially periodic units, each containing a relatively small number of cells, which are identical in the periodic units. Such a spatial periodicity is also found in the other optic ganglia.

In the honeybee the rhabdomeres are fused forming a rhabdom. They are not separated as in flies (e.g. Goldsmith 1962). Thus the rhabdomeres of the retinula cells are optically coupled (Varela 1970; Varela and Wiitanen 1970). The retinula cells are furthermore electric-

ally coupled (Shaw 1967), implying certain functional properties (Snyder 1973; Snyder and Pask, 1973). A similar (compared to flies) projection of retinula cell axons onto the Lamina and Medulla is found in the bee (Ribi, 1973). Spatial periodicity of cell groups also occurs in the bee.

A detailed description of the neuroarchitecture does not provide the information necessary to correlate the neural network with the behavioral responses. To date, these attempts have to be looked upon as working hypotheses which must be verified by optomotor and electrophysiological investigations and anatomical identification of the cells involved.

It may be mentioned that another promising line of research is that of correlating changes in behaviorally and electrophysiologically obtained responses with genetically controlled anatomical alterations. This is being pursued at Caltech by Benzer et al. and in Tubingen (Germany) by Goetz and Heisenberg.



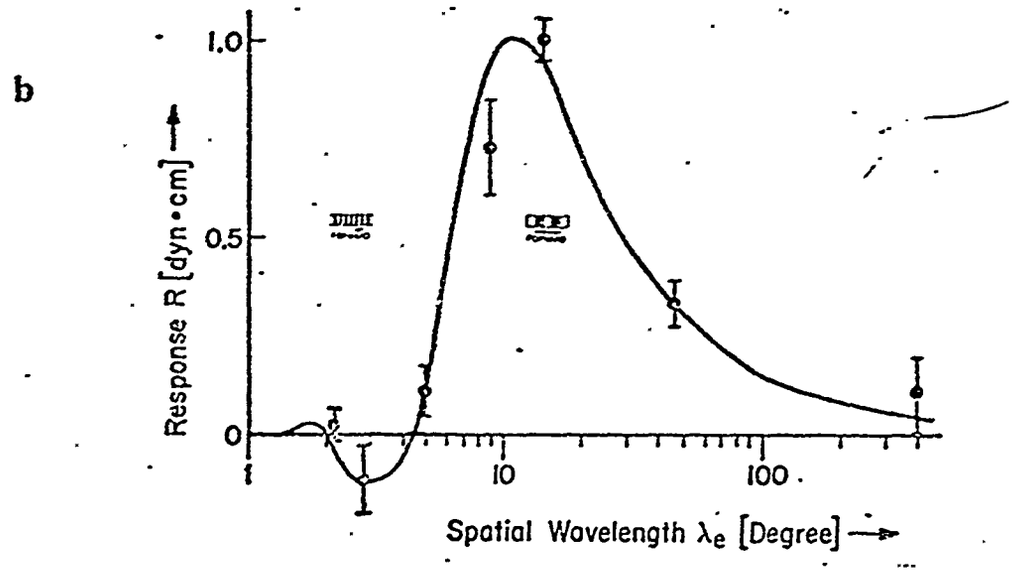


Figure 3a. Post -stimulus- time histogram of a directionally selective motion detecting neuron recorded extracellularly from the lobula of the housefly Musca domestica. Contralateral visual field; preferred direction: horizontal, back to front. Pattern wavelength: 3.6°; 14.4°.

In the extracellular recordings, these units usually had a spontaneous activity, sometimes as high as 20 spikes/sec. The data in this figure illustrate the incomplete resolution of a striped pattern by spatially fixed arrays of receptors (geometrical interference).

b. Torque elicited by fixed flying flies under comparable stimulus conditions. Parameter of the stimulus is the spatial wavelength of the pattern. Reversal of direction of reaction as shown for figure 3a for spatial wavelengths between 2° and 4°: predicted model response (continuous line) and experimental results (○) with standard deviation (vertical bars).

4. Electrophysiological Studies

This section is intended to give a condensed summary of our present knowledge derived from electrophysiological recordings. Not included is the perception of polarized light and the processing of this information in the visual system.

Extracellular recording from single units in the fly optic lobe was first reported by Bishop and Keehn (1966, 1967). Prior to this time only the retina had been studied by recording the electroretinogram (ERG), and intracellular potentials from the retinula cells (e.g. Kuiper and Leutscher-Hazelhoff, 1965; Burkhardt, 1964).

The initial extracellular studies were performed to find out if recordings could be taken from the neurons that are involved in the optomotor response. Units were found that responded similarly, compared to the (behavioral) optomotor responses, when tested under similar experimental conditions. When recorded extracellularly, most of these units had a spontaneous activity of 5-20 spikes per second. The striking feature of the response of these units is that they are excited by movement of an object in one direction (preferred direction), and inhibited by movement of the object in the opposite direction (null direction). The reaction decreases as the cosine of the angle of deviation of the direction of object movement from the direction of maximum response. Judged from extracellular recordings, these cells appeared to be located on the posterior surface of the lobulus (lobula plate).

Data obtained from extracellular recording of these units and of the behavioral optomotor response are shown in figure 3. We would like to point out an interesting observation regarding the reactions at long and short spatial wavelengths. A reversal of the direction of the response (relative to the direction of motion of an object) at short spatial wavelengths occurs in the behavioral optomotor response and in the response of these units. It is explained as being due to the incomplete resolution of a striped pattern by a spatially fixed array of sampling stations (Bishop, 1966; Eckert 1973). This phenomenon is usually called geometrical interference (Hertz 1934, Hassenstein 1950, Götz 1964). The contribution of the receptor system 7 and 8 to the response of these units was reported by McCann and Arnett (1972) but has to be

repeated and verified under the special experimental conditions reported by Eckert (1971). Other correlations between the responses of these cells and the optomotor response are: 1) the post stimulus time profile of the averaged spike rate and the torque elicited by the flying animal; a similar dependence upon 2) the spatial wavelength 3) the angular velocity of a striped pattern, 4) the angle from the maximum direction, 5) contrast of the pattern and 6) a similar dependence upon light intensity.

An examination of the spectral sensitivity of these cells indicated that the input to them was dominated by the 1-6 retinula cell system (Bishop 1969). In an examination of the spectral properties of the behavioral optomotor response Eckert (1972) found that the 7, 8 system contributes as well to the optomotor response.

Four sets of these motion units were found in each eye: preferred up, null down; preferred down, null up; and a similar set with direction of maximum response at right angles to the vertical. These cells respond to input from one entire compound eye -either a contralateral eye, or an ipsilateral eye. Additional studies defined more of the properties of these cells (McCann and Dill, 1969; McCann and Arnett, 1972). Mimura (1971, 1972) subsequently recorded from this area. It is difficult to tell if the cells he reports are these cells or different ones, since he has shown properties that do not have a unique interpretation. Intracellular identification will help in this matter.

Many types of cells have been recorded extracellularly (Bishop, Keehn, and McCann, 1968: Bishop, unpublished results; Eckert, unpublished results). Two interesting types of cells were reported by Arnett (1972). One responds to light flashes with a sustained response, the other only at the onset and offset of the light stimulus. The sustained units have a central excitatory On-region and two symmetrical, inhibitory Off-regions arranged along the horizontal axis (Arnett, 1972; Eckert 1974a, 1974b). These units are recorded in the first optic chiasma (in our experience) close to the anterior surface of the medulla. Arnett suggested that these cells were the second order monopolar cells of the lamina. There is some question as to the identity of these cells, since Jarvilehto and Zettler (1970, 1973) have recorded intracellularly

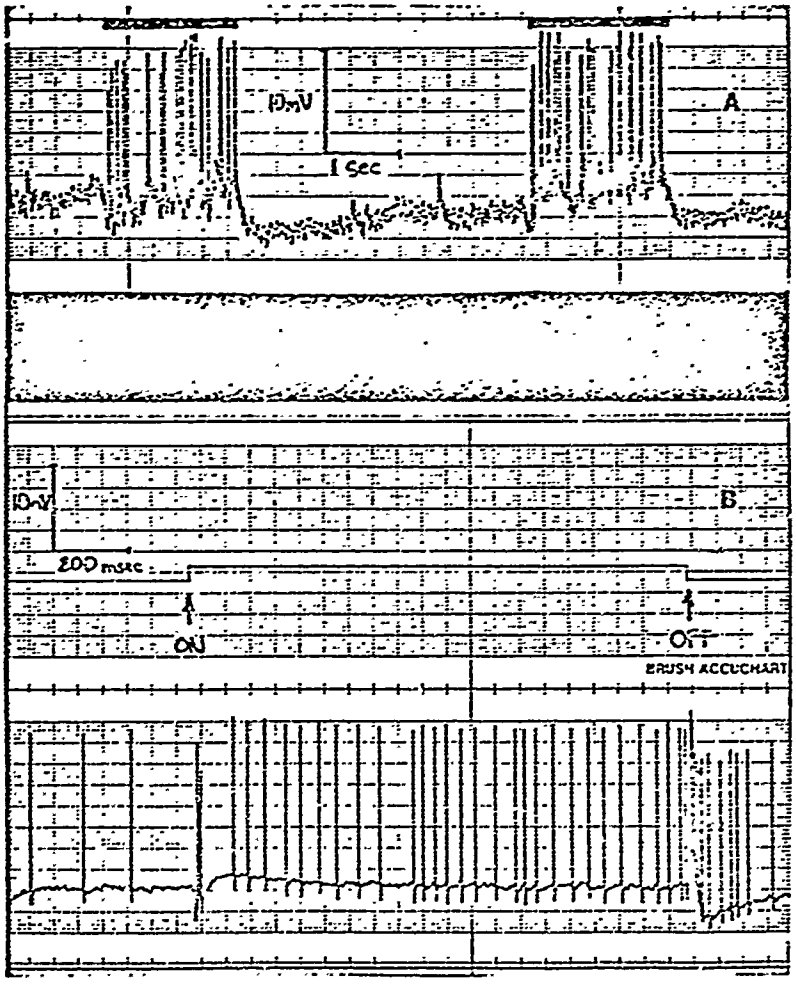


Figure 4. Intracellular recordings from cells in the lobula of the blowfly Phaenicia sericata. A. Sustained response to light. Bar indicates light is on. B. Sustained response to light on, but with transient responses at ON and OFF.

and subsequently stained from two types of second order monopolar neurons (L1, L2) in the lamina and along the axons (in the chiasma externa) and have not observed action potentials (see also Ioannides and Walcott, 1971). Obviously, intracellularly injected dye and subsequent identification will settle this controversy. Eckert (1974a,b) made an analysis of the nonlinear transfer characteristics by stimulating these fibers with light spots whose intensities were modulated in white noise fashion. We shall attempt to stain these fibers, too.

A question remains as to whether cells with binocular visual fields are present. Units have been recorded in the supraesophageal ganglion (Bishop, Keehn, and McCann, 1968) and in the lobula complex (Eckert, unpublished results) that appear to have binocular input. Intracellular injection of dye and anatomical identification will show whether these are the same fibers.

Lateral inhibition is an important phenomenon in visual sensory physiology. Obviously the directionally selective motion detectors exhibit lateral inhibition in the null direction. Somewhat more interesting is the observation that lateral inhibition is present in the preferred direction (Bishop, unpublished data). This is observed in the number of spikes evoked by light flashes in a two spot experiment.

An old and interesting idea in neurophysiology is that of efference copy, the idea that sensory input due to voluntary movement of the animal is accounted for in the nervous system. We have found that the motion cells respond during voluntary animal movement, which is consistent with Hassenstein's idea that the optomotor response is operative during voluntary movement.

Over the past year in this laboratory we have concentrated our efforts on intracellular recording. Some studies have been made by recording the retinula cell receptor potential. One study (Bishop, 1974) reports the presence of single-peaked spectral sensitivities in the uv and visible range of the spectrum in a bee-mimic fly, Eristalis tenax. The spectral sensitivities of retinula cells show a phenomenon which is still an unsolved puzzle. One type of retinula cell in many flies exhibits a double-peaked spectral sensitivity. This conflicts with our present knowledge about visual pigments causing the spectral

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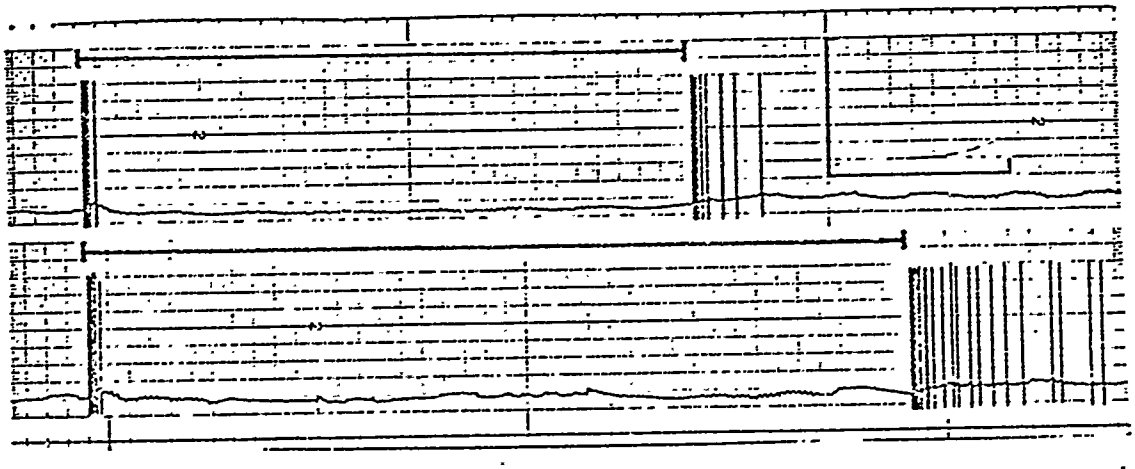

Figure 5. Intracellular recording from a cell in the lobula of the chalky mutant of the blowfly Calliphora erythrocephala. This cell showed no spontaneous activity and responded with a burst of action potentials at light ON and OFF. At a constant light intensity level the response at ON was constant, while the OFF response increased with the duration of the light flash. In the record shown above: ON: 9;9 spikes; OFF: 12; 25 spikes. Markers: 100mV., 0.5 sec. Resting potential 60mV. (recorded on FM tape and transferred to a strip chart recorder).

sensitivity. Several groups are working on this problem (Goldsmith et al./Yale; Hoffman, Langer et al. Bochum/W. Germany; Snyder, Horridge et al./Canberra, Australia; Bishop, Fernandez, Eckert/USC).

It has been reported frequently in the literature that the intensity response of retinula cells obeys a "log-linear" relationship. A white noise analysis of the retinula cell receptor potential has revealed that over a wide range of intensities the response is linear within a frequency band of approx. 5-30 Hz (Eckert and Bishop, 1974).

Intracellular recordings have been obtained from a large number of different types of cells (examples in figures 4,5,6, 7). Some of them have been stained intracellularly with procion yellow. Figure 8 shows a stained motion cell (Dvorak, Bishop and Eckert, 1974). Many more of these cells have to be stained before one can be confident that the entire cell with all its processes is stained. Only then can certain questions be answered. For example, does the contralateral cell extend across from one optic lobe to the other? How many motion cells are there? To what units in the medulla does the motion cell connect and hence from which units in the lamina and retina does it receive input? Dr. Stausfeld has narrowed the identification of the motion cell shown in figure 8 to three candidates on the surface of the lobula plate.

The motion cells have also been recorded extracellularly in the lobula of the honeybee (Kaiser and Bishop, 1970). Autrum and von Zwehl (1964) identified at least three types of photoreceptors by intracellular recording in bee retinula cells. Kaiser (1973) and Bishop (1970) disagree somewhat about how many of these photoreceptors contribute to the motion cells. From extracellular recording studies the motion cells in the bee are located on a region of the lobula analogous to the region from which they are recorded in the fly. According to the anatomical studies of Strausfeld as well this is deep in the bee optic lobe and on the surface of the fly optic lobe. Intracellular staining in the bee will supply additional information and complement the studies on the fly

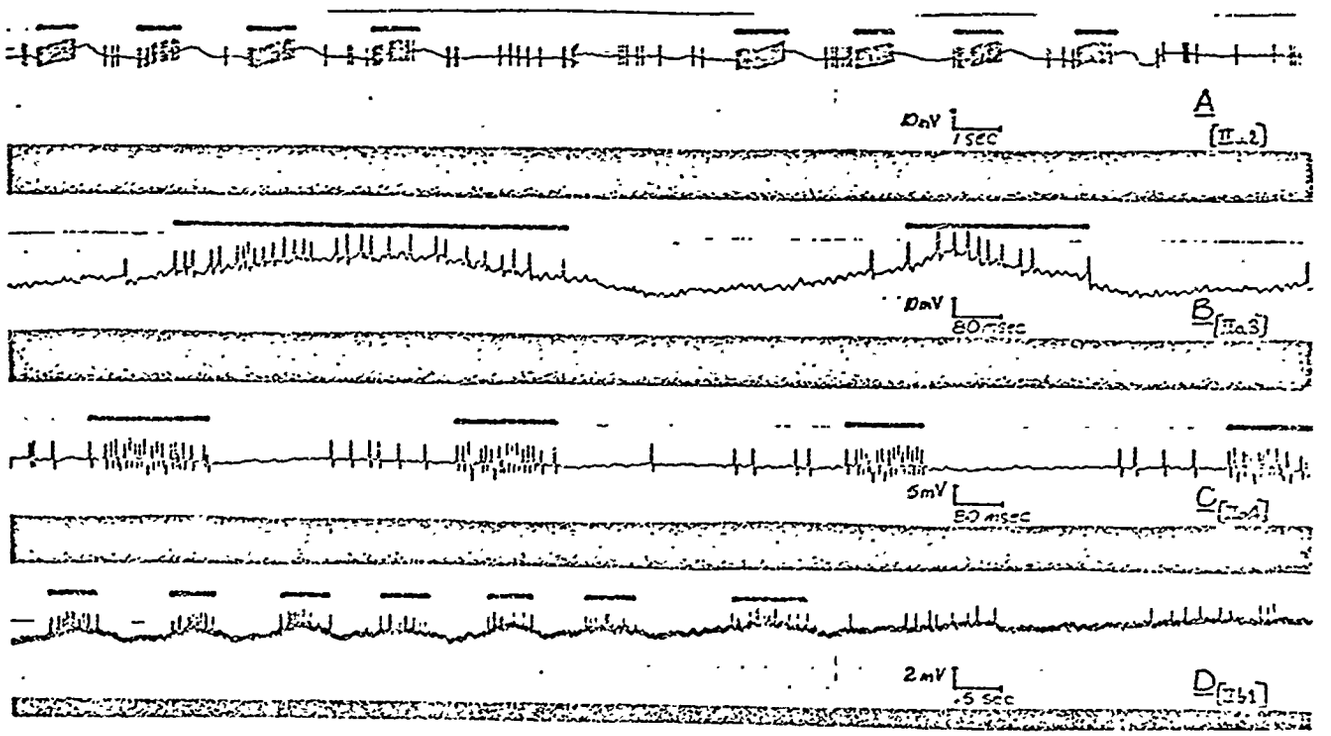

Figure 6. Intracellular recordings from directionally selective motion cells in the lobula complex of the blowfly Phaenecia seracata. Dark bars indicate movement of a striped pattern in the preferred direction. The pattern was moved in the null direction during the intervening periods. Recording was made directly onto a strip chart recorder, hence the action potentials are truncated. Numbers in brackets refer to preferred directions (Bishop et al., 1968).

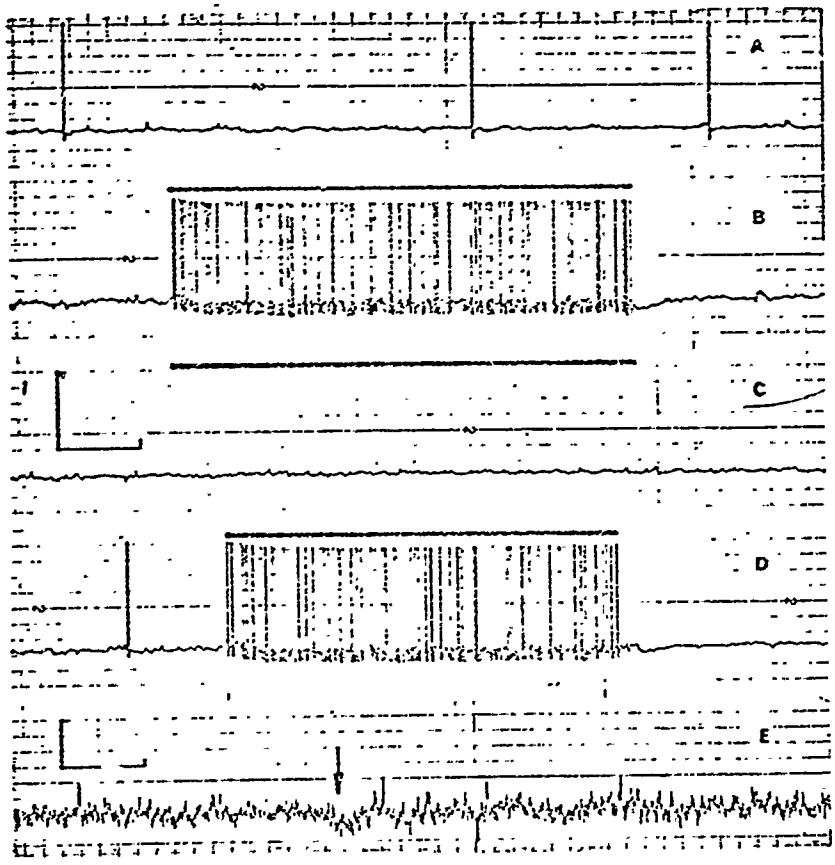

Figure 7. I racellular recording from a directionally selective motion detecting cell in the lobulus of the blowfly (preferred direction: dorsal to ventral). A. Spontaneous activity, pattern illuminated. B and D. Response to movement of a striped pattern (bars) in the preferred direction. C. Bar indicates movement of the striped pattern in the null direction. Markers in A-D: 60mV., 0.5 sec. E. Subthreshold activity; arrow indicates beginning of pattern movement in the null direction. Markers: 6mV., 0.5 sec.

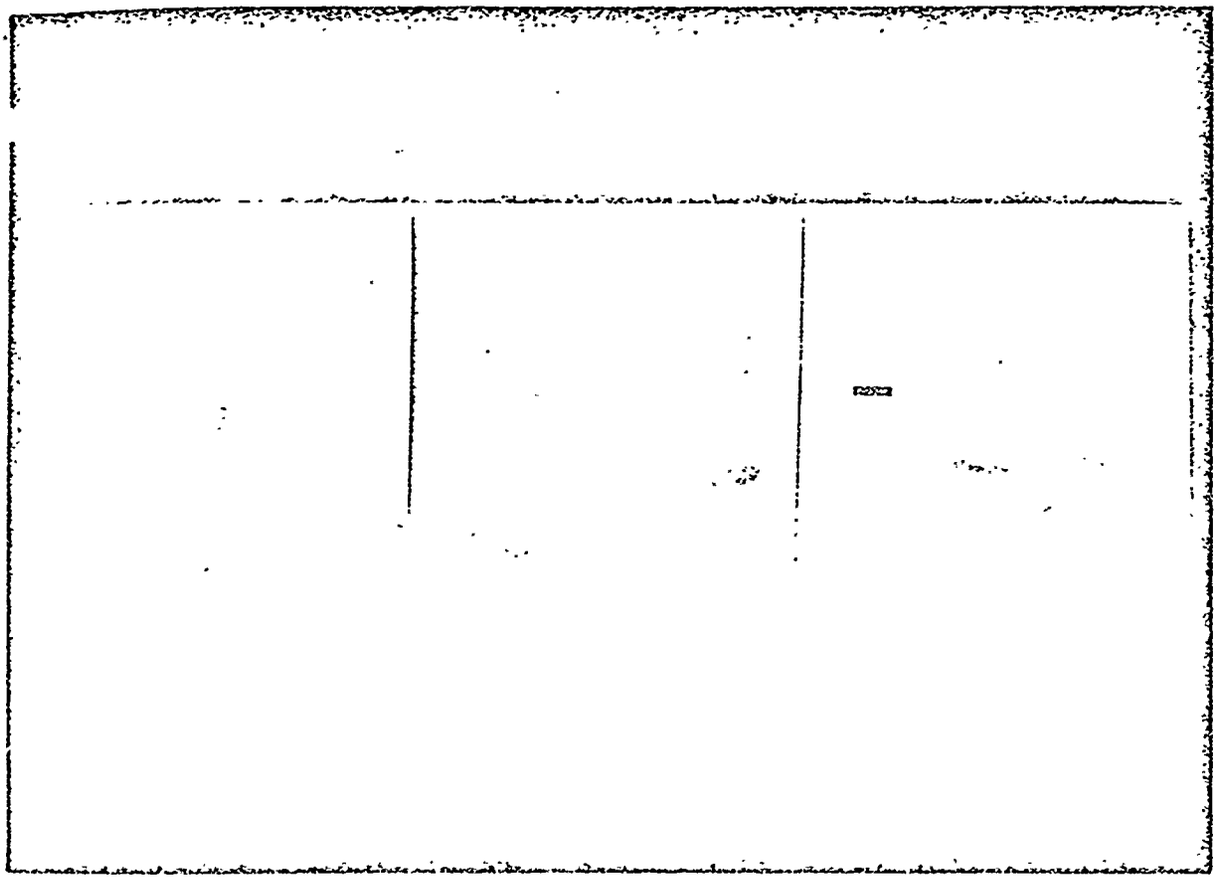

Figure 8. Photomontage of a horizontal cross section through the fly's head showing a directionally selective motion detecting cell into which the fluorescent dye procion yellow had been injected iontophoretically. This cell lies close to the posterior surface of the lobula plate, as indicated schematically in figure 1. The diameter of this cells averages approximately 4 micra; it has been traced a distance of 1300 micra, from the peripheral end of the lobula plate to the mid-brain. The visual field of this cell corresponded to the entire contralateral eye; preferred direction was dorsal to ventral (a down cell). Blowfly, Phaenicia seracata. Marker: 50μ.

motion detecting system.

Sustaining units similar to those found by Arnett in flies have also been recorded extracellularly from the bee (Bishop, 1972). These units receive information only from the green receptor. From the behavioral data it is obvious that chromatic information is transferred through the lamina to higher centers, but a neurophusiological explanation is difficult in view of the optical and anatomical mixing at the retinula level and in the lamina.

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